



A new Cretaceous orthopteran family of the Caelifera (order: Orthoptera) from Burmese amber of northern Myanmar

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Abstract

A new family of short horned grasshoppers, *Burmecaelidae* fam. nov., is described on the basis of a new species: *Burmecaelinus armis* fam., gen. et sp. nov. While any extant species can clearly be sorted into the Tridactylidea and Acrididea, the new fossil species presented here does not clearly match any of the two groups. The metafemora of the new family are apparently saltatorial and greatly inflated along its entire length, which is similar to extant and Mesozoic Tridactylidae and Ripterygidae. In contrast, the compound eyes are elongated and protrude from the head dorsally; the elongated area of the pronotum does not cover the abdomen. Although the morphology of the hind legs is shared with Tridactylidea, the shape of the head and abdomen are more similar to Tetrigoidea and Eumastacoidea. We suggest two hypotheses: (1) the new family emerged at the basis of the superfamilies Tridactylidea and Acridoidea early in Caeliferan evolution, or alternatively (2) the new family emerged within Tridactylidea, between the families Tridactylidae and Ripterygidae. The new family may have emerged when these families split. The phylogenetic placement of the new family needs to be further evaluated in the future based on more specimens.

Keywords Acrididea · Burmite · Caelifera · Fossil record · Tridactylidea

Introduction

Orthoptera are a medium diverse order of insects with about 30,000 extant species (Cigliano et al. 2022). They have an age of about 300 million years (Song et al. 2015), yet, their fossil record with about 900 described fossil species is not well explored. Much unstudied material is available in collections waiting for its discovery. Some recent interest has led to the description of several new fossil orthopteran species in twenty-first century (e.g., Heads 2009, 2010; Otte

2014; Uchida 2022). However, this is not true for higher level taxa. Most families of Caelifera (order: Orthoptera) were described before the first half of twentieth century and only a few families based on fossil specimens (e. g., † Bouretidae; Martins-Neto. 2003) have been discovered in the recent decades.

This may partially be owed to the still not fully resolved systematics of the group. While the relationships within the Ensifera are relatively well understood, many higher-level taxa within the Caelifera, especially the Acrididae with its sub-families, remain understudied and comprise many non-monophyletic groups (Song et al. 2018, 2020). Currently, the suborder Caelifera is split into two infraorders, Tridactylidea and Acrididea (e.g., Dirsh 1961, 1975; Sharov 1968; Song et al. 2015). The morphological differences between these two infraorders are distinctive; therefore, these higher taxa have long been recognized. Such classic taxonomic hypotheses are based on different character sets (Song et al. 2015), such as wing venation (Zeuner 1942; Sharov 1968; Gorochov 1995), external morphology (Blackith & Blackith 1968; Vickery & Kevan 1983), and the male phallic complex (Roberts 1941; Dirsh 1973; Eades 2000). Recently, systematic and genetic analyses also supported the classification of

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the two infraorders Tridactylidea and Acrididea (e.g., Grimaldi & Engel 2005; Song et al. 2015).

Although the extant species can clearly be sorted into the Tridactylidea and Acrididea, fossil species of the two families may not be as clearly matching any of the two groups and may combine morphological features of both Acrididea and Tridactylidea. Such intermediates possibly represent taxa at the basis of the split of these taxa or now extinct lineages, which were on a different evolutionary path than the survivors. Such fossil taxa may provide important insights into the early evolution of Caelifera.

Only a few families of Caelifera are known from the Mesozoic, which leaves a gap in our knowledge of orthopteran evolution. One commonly found group in Burmese amber, that shares some features with Caelifera, but most likely belongs to the Ensifera are the Elcanidae. However, most of the known fossils belonging to Caelifera stemming from Cretaceous Burmese amber deposits of Myanmar can be placed in the extant superfamily Tridactylidoidea (Heads 2009; Xu et al. 2020; Du et al. 2022).

In the present study, we examine an enigmatic orthopteran specimen from Kachin amber that has a unique combination of characteristics of the eyes, antennae, legs and genitalia. Although the morphology of the hind legs of the new species is similar to Tridactylidae and Ripipterygidae, the head, pronotum, and body shape are quite different from those of known Tridactylidae and Ripipterygidae species. Hence, we here describe a new genus and species from Burmese amber that cannot be placed within any recognized extant family of Caelifera and therefore we propose a new family for it.

Materials and methods

The ambers were excavated from a mining locality near Tanai Village (26° 21' N, 96° 43' E) in the Hukawng Valley of northern Myanmar (Cruikshank and Ko 2003; Dong et al. 2015; Uchida 2022). Although the accurate geo-coordinates of the mining site are unknown because of mix-up of samples from local miners, the age of amber from Tanai Village has been estimated at approximately 99 Ma (98.8 ± 0.6 ; earliest Cenomanian) based on the U–Pb dating of zircons from the volcanoclastic matrix of the amber (Cruikshank and Ko 2003; Shi et al. 2012). According to Westerweel et al. (2019), the ecosystem reflected in Myanmar/Burmese amber was part of the Burma Terrane, which broke off from Gondwana in the Late Jurassic–Early Cretaceous (Heine et al. 2004; Heine and Müller 2005) and subsequently drifted northwards and rotated clockwise before it reached its present-day location (Westerweel et al. 2019). The amber piece was polished to a final size of 17.5 mm × 1.23 mm × 2.9 mm, followed by examination

using a Shimazu-Rika stereomicroscope and a CANON EOS6D Mark2 camera. Microphotographs of approximately 10 focal layers of the same specimen were combined with CombineZM (Hadley 2008). The drawings and measurements of the specimen were conducted using Adobe Illustrator 25.2. The format of the descriptions follows Xu et al. (2020), Du et al. (2022), and Uchida (2022). The fossil in the present study is well preserved; however, the left antenna, left meta-tibia and left tarsus are damaged.

Systematic paleontology

Order **Orthoptera** Olivier, 1789

Suborder **Caelifera** Ander, 1936

Family **Burmecaelidae** fam. nov.

Type genus. Burmecaelinus gen. nov.

Figures 1, 2, 3, 4, and 5

(urn:lsid:zoobank.org:act:D6D5B51C-5D65-4427-8134-150D9C1B05E2)

Etymology. The family name was derived from the Burmese amber of the fossil resin at Hukawng valley (*burmese*) and the word base of the suborder name (*Caelifera*). Gender female (probably). Nymph (probably).

Diagnosis. Head: hypognathous; with large compound eyes, elongated and protruding from the head dorsally, with very narrow fastigium; antenna very short, three-quarters length of the head dorsally, moniliform, 6 segments visible (slightly damaged); ocelli absent. Thorax: a rugged and saddle shaped pronotum, with convex anterior and posterior lateral margins, trapezoid shape dorsally with posterior margin of dorsal side nearly twice (approx. 1.7 times) wider than anterior margin of pronotum, not extending over abdomen. Pro-legs: pro-tarsi one segment, with two tarsal pads in basal area. Hind legs: apparently saltatorial; meta-femur slightly shorter than abdomen and greatly inflated along its entire length, with prominent dorsal carina; external genicular lobe prominent, smooth, with several irregularly spaced setae; meta-tibia slightly shorter than meta-femur, very slender, two apical spurs and six subapical spurs visible; meta-tarsus subquadrate in section, with two prominent apical denticular processes ($dent^L$ and $dent^R$).

Genus **Burmecaelinus** gen. nov.

Type species. Burmecaelinus armis gen. et sp. nov., by monotypy.

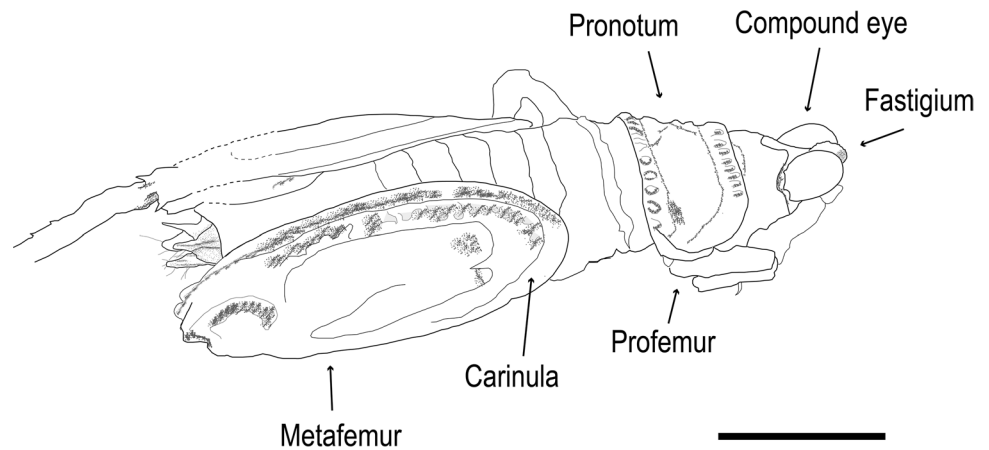
Figures 1, 2, 3, 4, and 5

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Fig. 1 *Burmecaelinus armis* fam., gen. et sp. nov., holotype (UMIT MA33905). Photographs of right (lateral), left (lateral), and dorsal side of specimen. Scale bar: 1.0 mm

Fig. 2 *Burmecaelinus armis* fam., gen. et sp. nov.. Detail of specimen of dorsal and right lateral sides. Dotted lines represent reconstructed areas. Scale bar: 1.0 mm



Etymology. The generic name was derived from the Burmese amber of the fossil resin at Hukawng valley (*burmese*) and word base of the suborder name (*Caelifera*). Gender female (probably). Nymph (probably).

Diagnosis. As for family.

Burmecaelinus armis gen et sp. nov.
 Figures 1, 2, 3, 4, and 5

(urn:lsid:zoobank.org:act:13D87FB5-D44C-4E7F-BC27-CC56FB97687C)

Etymology. The species name was derived from Latin and refers to the “armor” like pronotum and hind legs.

Locality and horizon. Amber-mine near Tanai Village in the Hukawng Valley of northern Myanmar; lowermost Cenomanian, middle-Cretaceous.

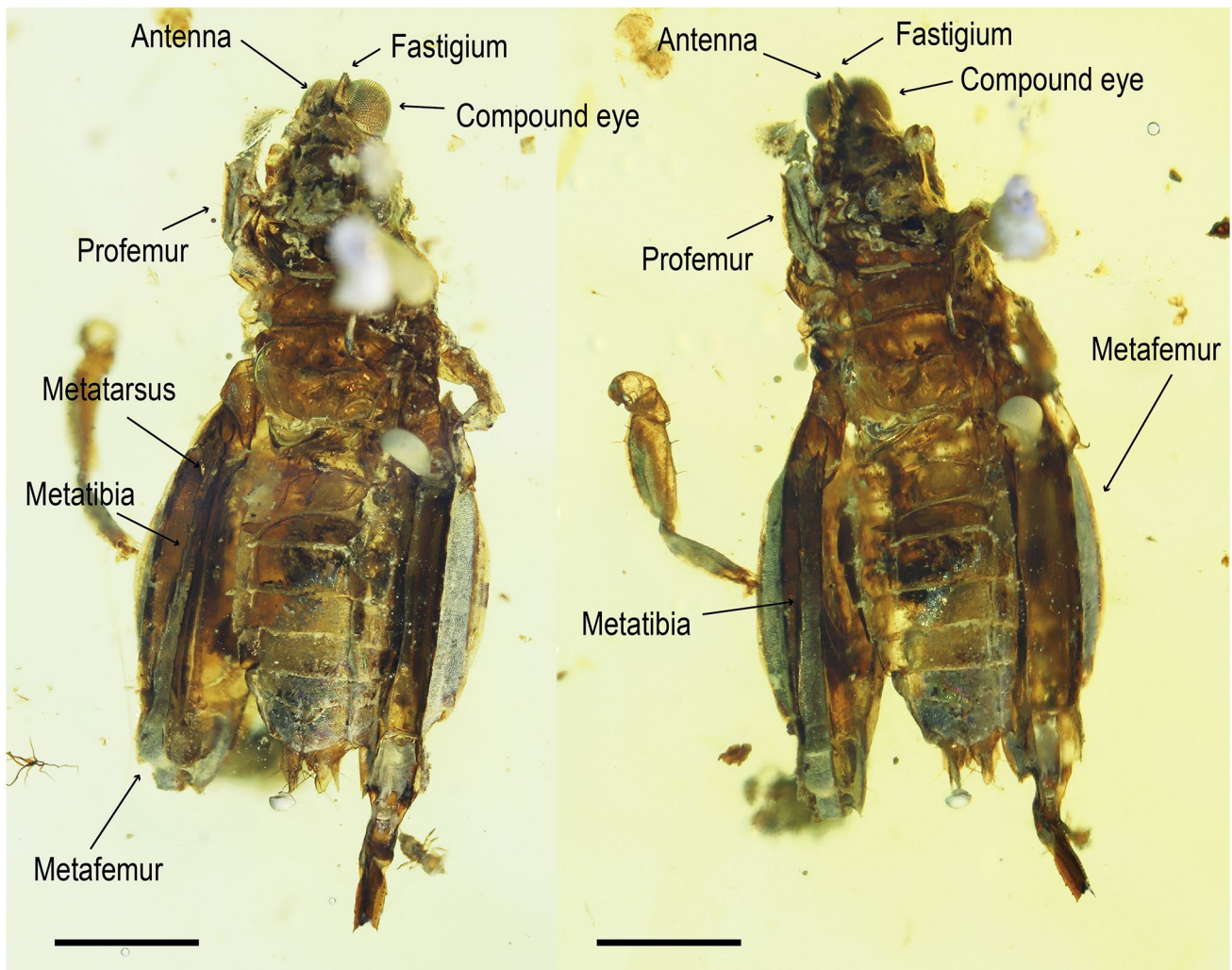


Fig. 3 *Burmeacelinus armis* fam., gen. et sp. nov., holotype (UMIT MA33905). Photographs of ventral side of specimen. Scale bars: 1.0 mm

Holotype. Nymph (probably) Female (probably), deposited under number UMUT MA33905 at the University Museum, The University of Tokyo, Japan.

Description. Characteristics as listed under generic description.

Body with no wings (probably nymph); length of body 3.81 mm, length of body including cerci 4.16 mm; length of pronotum 0.61 mm.

Head (Figs. 1, 2, 3, and 4): hypognathous, longer than wide; large eyes elongated and protruding from the head dorsally, 0.38 mm long dorsoventrally and 0.27 mm wide laterally, with very narrow fastigium; ocelli not observed; length of antenna 0.69 mm, very short, three-quarters length of the head dorsally, base in the mid-point of head dorsally, antennal flagellum moniliform, 6 segments visible (somewhat robust, slender basally and broad apically), with each antennomere covered by rugged surface, scape cylindrical,

antennal cavities not observed (slightly damaged), flagellomeres apical-most segment gradually narrowed towards the apex. Base area of antennae in mid of frons of head dorsally.

Thorax (Figs. 1, 2, 3, and 4): pronotum 0.61 mm long, lateral lobes 0.37 mm high, with a rugged surface and saddle shaped, rectangular shaped laterally, anterior and posterior lateral margins slightly convex, trapezoid shape dorsally, with posterior margin of dorsal side (1.47 mm) nearly twice (approx. 1.7 times) wider than anterior margin (0.88 mm), not extending over abdomen in dorsal area.

Abdomen (Figs. 1, 3, and 4): long, two-thirds the length of body, with 11 segments visible (fourth and fifth segments damaged, therefore number of segments may be fewer); cerci one-segmented, cercus slender with several long setae; epiproct and subgenital plates visible, subgenital plate somewhat curved on ventral side distally, gradually narrowed apically, only slightly shorter than cerci, all other genital structures hidden.

Fig. 4 *Burmecaelinus armis* fam., gen. et sp. nov.. Detail of head (A and B), pronotum (A), and genitalia (C and D). Dotted lines represent reconstructed areas. Scale bars: 0.5 mm

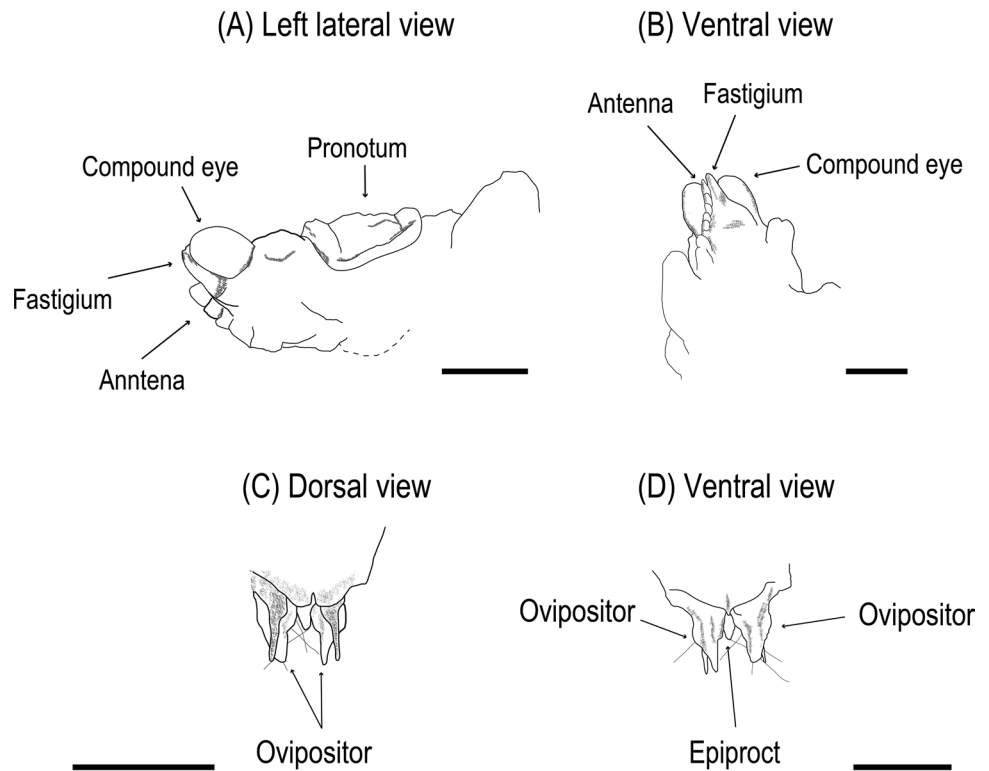
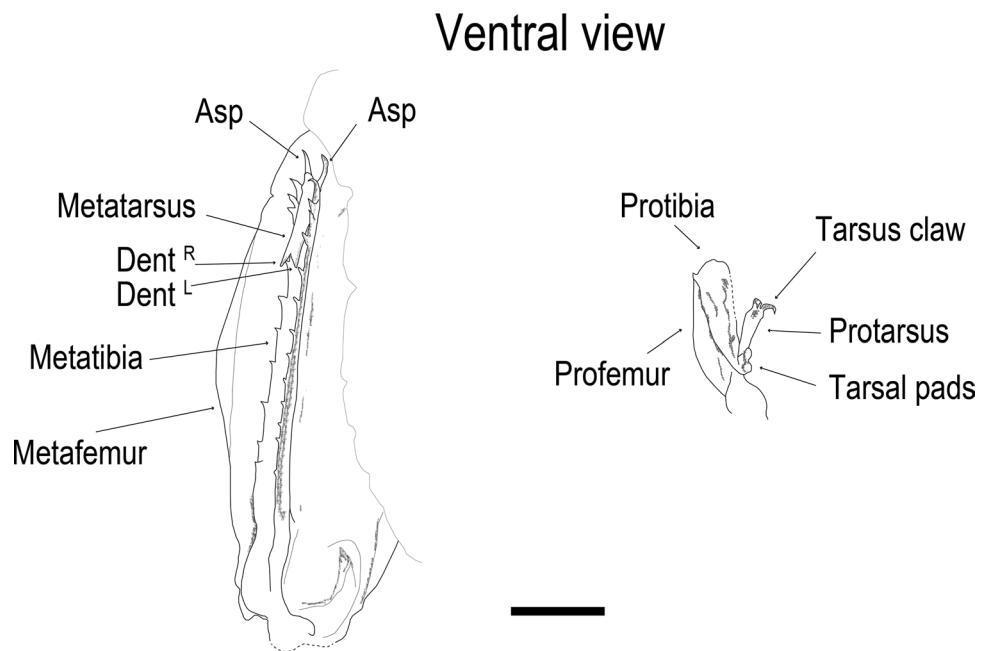


Fig. 5 *Burmecaelinus armis* fam., gen. et sp. nov.. Detail of femur, tibia, and tarsus of pro- and hind legs. Scale bar: 0.5 mm. Apical spurs (asp)



Legs (Figs. 2, 3, and 5): pro-thoratic legs, pro-femur 0.67 mm length, broad with several long ventral setae, slightly narrowed basally; pro-tibia relatively slender, inflated distally with a sparse cover of long setae; protarsus one segment, broad apically, tarsal claws apically

elongate, curved distally, with two tarsal pads in basal area; arolium not visible. Meso-thoracic legs: meso-femur 0.82 mm length longer than pro-femur and broader, basally narrow and distally broad with two carinae, with sparse short setae; meso-tibia and meso-tarsus damaged.

Meta-thoracic legs, meta-femur apparently saltatorial, 0.82 mm length, slightly shorter than abdomen and greatly inflated along its entire length, with prominent dorsal carina; external genicular lobe prominent, smooth, with several irregularly spaced setae; meta-tibia slightly shorter than meta-femur, very slender, two apical spurs and six subapical spurs visible, no swimming tibial lamellae; meta-tarsus subquadrate in section, with two prominent apical denticular processes (dent^L and dent^R).

Discussion

Fossil specimens are accepted as important source of information for phenotypic evolution, as well as for dating of phylogenies (Donoghue 2005; Grimaldi & Engel 2005; Heads 2009; Moritz & Wesener 2021; Haug et al. 2022). The present study describes a new family (Burmecaelidae fam. nov.), which is different from previously known Caelifera species.

A new family with a unique combination of traits

In particular, this new family shows unique morphologies placing it somewhere in between the two known super-families of Caelifera: while the morphology of the hind legs is shared with Tridactylidae, head and pronotal features are quite different. The compound eyes are elongated and protrude from the head dorsally and the elongated area of the pronotum does not cover the abdomen. The metafemora of the new family are apparently saltatorial and greatly inflated along their entire length, similar to Tridactylidae and Ripipterygidae (Brullé 1835; Ander 1939; Xu et al. 2020; Du et al. 2022). In addition, the meta-tarsus has two apparently large dents, a feature also shared with several species of these two families. However, the morphology of the pro-legs and of some parts of the hind legs characteristic for Tridactyloidea are not shared with the new family. Both the pro-femora and pro-tibiae of the new family are relatively slender compared to other tridactylid species that have very robust and broad pro-tibiae in adaptation to their life style. Extant pygmy mole crickets inhabit rather humid environments, often along water bodies, where they dig into the soil and construct small burrows in moist sandy ground (Günther 1995). In addition, most extant species of the subfamily Tridactylidae are armed with two rows of swimming tibial lamellae on their meta-tibiae in order to swim on the water surface. However, no Tridactylidae found in Kachin amber so far possess swimming plates (Xu et al. 2020; Du et al. 2022), suggesting that they had not obtained the ability of moving across water surface at that time. Furthermore, the new family has two large apical spurs on the meta-tibia, which also similar to extant Tridactyloidea species.

The morphology of both head and abdomen in the new family Burmecaelidae are quite different from other Caelifera taxa. In particular, the compound eyes are strongly elongated and protrude clearly above the head dorsally; a very narrow fastigium is visible. According to our knowledge, the structure of the compound eye of the new family is not shared with any known Ensifera and Caelifera species. The genus *Teredorus* in Tetrigoidea has protruding compound eyes (Hancock 1907; Deng et al. 2014) that are slightly similar with the new family. Similarly, compound eyes in many extant species of Eumastacoidea are protruding above the head (Rowell & Perez-Gelabert 2006; Song 2010). Also, the head of Pyrgomorphoidea species protrudes dorsally, which is slightly similar to the new family. The fastigium of the new family is flat and very narrow dorsally, which resembles the morphology of the fastigium in *Teredorus* species and some other species in Tetrigoidea (Hancock 1907; Deng et al. 2014). However, the compound eyes of *Teredorus*, Eumastacoidea, and Pyrgomorphoidea species are globose or pear-shaped.

Antennomeres are very short, broad and have a rugged surface in the new family. The apical-most segment of the flagellomeres is gradually narrowed towards the apex. The basal area of the antennae is in the mid-part of the frons of the head dorsally below the compound eyes. This setup is somehow similar with that of extant species of Ripipterygidae (e.g., *Ripipteryx gorgonaensis*). In addition, many species of Eumastacoidea and the genus *Crypsicerus* in Lathiceridae have a similar antennal morphology with the new family (Dirsh 1954, 1965; Rowell & Perez-Gelabert 2006). Furthermore, the new family has a rugged and trapezoid shaped pronotum, which does not extend over the abdomen, similar to the pronotum of Acridoidea species. According to our knowledge, this unique combination of morphological features does not resemble any group within Ensifera and Caelifera. Overall, we have found no evidence for a close relationship of Burmecaelidae to other Ensifera and Caelifera taxa.

Hypothetical phylogenetic relationships

The new family has unique features not resembling any other taxonomic group closely, yet the combination of morphological traits allows to generate hypotheses on its phylogenetic placement. Here, we suggest two hypotheses for the placement of the new family Burmecaelidae: (1) The new family emerged at the basis of the superfamilies Tridactyloidea and Acridoidea early in Caeliferan evolution (Fig. 6; Hypothesis 1). The morphology of legs, particularly, hind legs are shared with Tridactyloidea. However, head shape and abdomen are quite different from Tridactyloidea, and are more similar to Tetrigoidea and Eumastacoidea. Therefore, the new family Burmecaelidae may have symplesiomorphies of head and

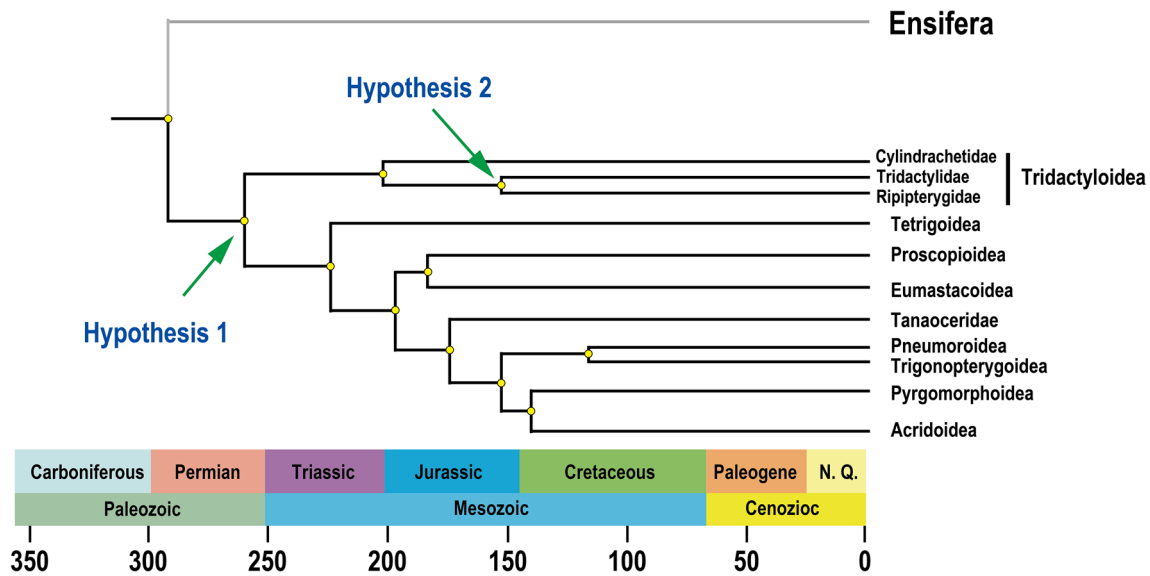


Fig. 6 Hypotheses of phylogenetic splitting event of *Burmecaelinus armis* fam., gen. et sp. nov. Figure modified from Song et al. 2015 (geological boundaries updated). A divergence time-estimate analysis of Orthoptera based on mt-genome data and nine fossil calibration points using BEAST. Yellow circles on nodes indicate posterior probability values over 95 according to Song et al. 2015. The present study suggests two hypotheses for the placement of the new family Burmecaelidae: (1) The new family emerged at the basis of the super-

families Tridactyloidea and Acridoidea early in Caeliferan evolution. The morphology of hind legs is shared with Tridactyloidea. However the head and abdomen shape are quite different from Tridactyloidea, which are more similar to Tetrigoidea and Eumastacoidea. (2) The new family emerged within Tridactyloidea, between the families Tridactylidae and Ripterygidae. The morphology of antennae and hind legs in the new family resemble at least superficially extant pygmy mole crickets

abdomen with Acridoidea. (2) The new family emerged within Tridactyloidea, between the families Tridactylidae and Ripterygidae (Fig. 6; Hypothesis 2). The morphology of antennae and hind legs in the new family resemble at least superficially pygmy mole crickets (Tridactylidae and Ripterygidae). These two families have long been recognized because of the distinct morphological differences. The new family may have emerged when the families split, but while the other two families persisted Burmecaelidae became extinct. In addition, the new species has a 2–2–1 tarsal segmentation, which is a distinct character shared between the new family and Tridactyloidea. This trait is an important character that distinguishes Tridactyloidea from other caeliferan species. While the age of the fossil at hand would rather support the second hypothesis, the phylogenetic placement will have to be further evaluated in the future, preferable when additional specimens become available.

Conclusion

Burmecaelinus armis fam., gen. et sp. nov. is described from mid-Cretaceous Burmese amber. In the present fossil, most parts are exceptionally well preserved enabling a critical

evaluation of most morphological traits. As the new genus and species did not fit into any of the established higher level taxa, a new family is described. As new material is discovered, a comprehensive re-analysis of the classification of Caelifera, especially of the known fossils will be required.

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Author contributions The corresponding author (KU) is responsible for ensuring that the descriptions are accurate and agreed by all authors. KU and MH conceived of and designed the study. KU collected the data. KU, MH, and UK wrote the first draft of the manuscript. All authors contributed to revisions.

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Data availability The amber fossil was deposited under number UMUT MA33905 at the University Museum, The University of Tokyo. Qualitative descriptions and images of specimen are shown in the present paper.

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